10-1981

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ABSTRACT

A nonlinear least-squares procedure is developed to estimate harvest rate and differential vulnerability in wildlife populations that are harvested with 1 segment of the population more able than another. The method requires age data by category from a series of harvests, plus information on accumulated harvest effort, and assumes that the nonharvest mortality rate is the same for the categories. The data need not be from consecutive harvests, as long as the effort is known for missing Monte Carlo simulations were done to verify the estimation procedure. An example shows the application of the method to moose (*Alces alces*) harvest data from Ontario.

Age-structure data obtained from big-game harvests are frequently employed to measure mortality. However, Gill (1953), Caughley (1974), and others have cautioned that these data should not be relied upon, because many assumptions basic to the usual analyses (Eberhardt 1969, Caughley 1977) are violated and spurious results may be derived. This paper presents a statistic that avoids most biases while providing a direct estimate of the proportion of a population removed by hunters.

Harvest depends on the abundance of the exploited population, the ease of capture of the individuals, and the effort exerted in harvesting. Vulnerability frequently varies among individuals, often because of systematic differences based on size, age, or sex. Given appropriate data, such differences may be used to estimate the population size and rate of harvest.

Methods that rely on the selective removal of 2 different types of animals with concomitant changes in ratio have been widely used to estimate population sizes and survival rates. Chapman (1955 developed a stochastic model of what is now known as the change-in-ratio (CIR) method. In its simplest form, the CIR method assumes that the population is closed, that the ratio of the 2 classes can be estimated before and after a selective removal, and that removals from the 2 classes are known. Special cases where 1 or more of these assumptions are not met were considered by Chapman and many others (e.g., Chapman and Murphy 1965, Paulik and Robson 1969). Lander (1962) and Chapman and Murphy (1965) extended the CIR method to a situation in which the 2 types of animals are subject to mortality between the 2 sampling periods that establishes the ratio of the animals. The number of animals removed is assumed to be known. The estimates of mortalities and animal abundance are obtained by an iterative procedure. A good review of available methods is given by Seber (1973).

In many wildlife populations the total harvest is not known, natural mortality cannot be estimated, and the ratio of the 2 classes in the living population cannot be established with accuracy. However, ratios of classes in the harvest can be estimated, and good estimates of the harvesting effort are frequently available. Fraser (1976, unpubl. data) observed that a gradual change in the male-female ratio in the harvest can be used to estimate the rate of harvesting, if the harvest rate is relatively constant over time. The analysis is particularly simple if the 2 classes are equally abundant initially, and then are subjected to a series of harvests in which 1 class is consistently more vulnerable than the other. In this case the number of harvests required for the 2 classes to become equal in the harvest sample depends largely on the rate of harvesting and only slightly on the relative vulnerabilities of the classes.

In the present paper we extend this concept and develop a technique to estimate the harvest rate in a more general case when the harvest rate is changing. The technique gives an estimate of the harvesting rate and the size of the 2 classes and associated variances.

Data requirements of the present method are much less stringent than those of the conventional selective-removal methods. Our method does not re-quire separate samples to estimate the ratio of the 2 classes, or that the numbers of animals removed be known. Given a species with differential vulnerability of 2 classes, the method assumes that the ratio of the 2 classes of removals is known by age for a series of removal periods, that the mortality between the removal periods is the same for the 2 classes of animals, and that the actual ratio of the 2 classes in the population can be determined at 1 time, preferably before the beginning of the selective exploitation. If removals are known exactly, then the abundance of the 2 classes in the exploited population can also be estimated.

We are grateful to D. S. Robson for helpful comments and, in particular, for pointing out the close similarity between the least-squares method and the maxi-mum-likelihood method. C. D. MacInnes made valuable suggestions on the paper, and the Ministry of Natural Resources staff in Thunder Bay kindly supplied the data for the examples.

APPLICATION TO WILDLIFE DATA

The method appears applicable to certain populations of several wildlife species. Among black bears (*Ursus americanus*), the sex ratio at birth is approximately 1:1 (Rogers 1977). However, removal by man is strongly biased toward males (e.g., Gilbert et al. 1978), causing a characteristic change with age in the harvest sex ratio (Bunnell and Tait 1980).

Reindeer (*Rangifer tarandus*) have an approximately 1:1 sex ratio at birth (Nowosad 1975). In a hunted population studied by Reimers (1975), the harvest sex ratio became progressively biased toward females at older ages because of preferential shooting of males.

Our most detailed studies have centered on North American populations of moose in Ontario, Quebec, and Nova Scotia, where both sexes are hunted. The hunting season in these areas commonly coincides with part or all of the rutting season, when males are apparently more active and vulnerable to hunting (Pimlott 1959). The moose taken by hunters can be sampled and classified as to sex. Reasonably accurate methods of age classification can be applied to determine the sex ratio by age in the harvest, although with some loss of precise cohort identity (Gasaway et al. 1978).

The sex ratio of harvested calves is believed to be representative of the actual calf sex ratio in the population at the time (Haagenrud and Lordahl 1979). In Ontario the calf harvest sex ratio is consistently close to 1:1. For example, 51.9% of 3,226 calves reported shot in Ontario between 1967 and 1972 were males (Fraser 1979). Some preponderance of male calves has been reported in Scandinavian countries (Haagenrud and Lørdahl 1979).

In lightly hunted areas in Ontario, Quebec, and Nova Scotia, males predominate in the harvest at all adult ages, but heavily hunted populations show a steady decline with age in the proportion of males in the harvest (Fraser 1976; M. Crete and D. Fraser, unpubl. data). One explanation is that the change with age in the harvest sex ratio is caused by selective removal of males through hunting, not by different rates of nonhunting mortality or by changes with age in sex differential vulnerability to hunting.

Harvest results can occasionally be compiled for a particular cohort over a number of years. However, this is usually unsatisfactory because the methods of sampling harvested moose and the methods of estimating moose ages have rarely been consistent throughout the life of a cohort (Addison and Timmermann 1974). Results from a single hunting season are more readily available and less susceptible to such bias. This method can be applied to both cohort and single-season harvest data.

THE METHOD

The following notation will be used:

m_i = number of males in a given cohort at beginning of the i^{th} season,

f_i = number of females in a given cohort at the beginning of the i^{th} season, and

i = the first season in which the males are more vulnerable to hunting.

For moose, i = 1 usually occurs when the cohort is 1.5 years old. We will as-sume that m_1/f_1= 1 at the beginning of the first season. To express the expected harvest as a function of hunting effort, or number of hunters, statistical searching theory can be applied (e.g., Paloheimo 1971). Let

$p_{\text{m}}\Delta t$ = the probability that a hunter sights and kills a specific male moose in a short time interval, Δt, and

$p_{\text{f}}\Delta t$ = the corresponding probability for a female moose.

The expected number of males killed by 1 hunter in Δt is then equal to $p_{\text{m}}\Delta t$ multiplied by the number of males, and the total number of males expected to be killed by 1 hunter during the i^{th} season is [1 – exp(–p_{m})]m_{i}, where the season length is taken as our time unit and exp stands for exponentiation. Let

$H_{m,i}$ = number of males harvested during the i^{th} season,

$H_{f,i}$ = number of females harvested during the i^{th} season,

e_i = units of harvesting effort, expressed as thousands of hunters in the following discussion.

The total harvest of males and females by e_i units of effort is

$$E(H_{m,i}|m_i) = [1 - \exp(-p_m e_i)]m_i$$
$$E(H_{f,i}|f_i) = [1 - \exp(-p_f e_i)]mf_i, \qquad (1)$$

provided that the other sources of mortality during the hunting season are negligible. Because the moose-hunting season is usually short, we will ignore mortality not related to hunting during that season. The sex ratio of animals that are wounded and later die is probably the same as the ratio in the harvest. Hence, mortality due to crippling is included in our estimates.

The eqs. (1), often referred to as the catch equations, are widely used in fisheries work, and go back to Baranov (1918) and Ricker (1940). In the fisheries literature, the parameters p_m and p_f are called catchability coefficients; they are independent of the abundance of animals.

Although the derivations of the eqs. (1) in statistical searching theory presuppose a random (Poisson) search, they remain valid under much wider conditions, namely when either hunters or animals are randomly distributed (for further discussion see Paloheimo and Dickie 1964). If a rule such as a bag limit is imposed on searching or hunting, the basic eqs. (1) must be modified. If, however, the number of hunters reaching the bag limit is relatively small compared with the total number of hunters, say <20%, the effect of the bag limit can be safely ignored, as we have done here.

Let S_a = the annual survival of moose (both male and female), excluding the mortality due to hunting. We will apply this as a survival rate from the end of 1 hunting season to the beginning of the next. We are specifically assuming that the survival rate is the same for both males and females. The use of a single symbol, S_a, for survival in each year is for simplicity only; although it implies that off-season survival does not depend on the year i, the results in no way de-pend on this assumption.

Survival rates for the hunting season are obtained from $\exp(-p_m e_i)$ and $\exp(-p_f e_i)$ for males and females, respectively [eqs. (1)]. The expected numbers of moose at the beginning of the i^{th} season are now related to the numbers at the beginning of the first season, m_1 and f_1 as follows:

$$E(m_i) = m_1 \exp(-p_m \sum_{j=1}^{i-1} e_j)\, S_a^{i-1} \qquad (2)$$

$$E(f_i) = f_1 \exp(-p_f \sum_{j=1}^{i-1} e_j)\, S_a^{i-1}$$

Expected numbers of moose harvested each year can now be obtained by combining (1) and (2). Dividing the numbers of males by the numbers of females, arrive at an expression for the expected sex ratio in the harvest

(3)

$$E\left[\frac{H_{m,i}}{H_{f,i}}\right] = m_1 \exp\left(-p_m \sum_{j=1}^{i-1} e_j\right)[1 - \exp(-p_m e_i)]/f_1 \exp\left(-p_f \sum_{j=1}^{i-1} e_j\right)\left[1 - \exp\left(-p_f e_i\right)\right]$$

All estimates will be based on the above equation.

For descriptive purposes we may define the population harvest rate simply as the average of the male and female harvest rates. It is the fraction of the total population harvested when males and females are equally abundant:

$$\text{population harvest rate in year } i = 1 - \tfrac{1}{2}[\exp(-p_m e_i) + \exp(-p_f e_i)]. \qquad (4)$$

Male vulnerability may similarly be defined as the probability that the animal killed is male, given equally abundant sexes:

$$\text{male vulnerability in year } i = [1 - \exp(-p_m e_i)]/[2 - \exp(-p_m e_i) - \exp(-p_f e_i)]. \quad (5)$$

STATISTICAL PROCEDURES

Both harvest rate (4) and vulnerability (5) vary from year to year, depending on the amount of hunting effort and on other variables, such as weather. The parameters that are presumably not affected by the fluctuating hunting activities are the probabilities of capture of 1 moose of either sex by 1 unit of hunting effort, i.e., p_m and p_f. These may be estimated from eq. (3) using a weighted nonlinear least-squares procedure, for which several "canned" programs are available (e.g., BMDP; Dixon and Brown 1977). This procedure can be shown to be, for all practical purposes, equivalent to a maxi-mum-likelihood method (D. Robson, pers. commun.).

The estimates of the probabilities of capture, p_m and p_f, will be correlated. It is therefore preferable to set new parameters for eq. (3). We define p as average probability of capture of 1 moose by 1 unit of hunting effort, and u as differential vulnerability,

$$p = \tfrac{1}{2}(p_m + p_f) \quad \text{and}$$
$$u = \tfrac{1}{2}(p_m - p_f)$$

Then:

$$p_m = p + u$$
$$p_f = p - u \quad (6)$$

Strictly speaking, p is the average probability only when both sexes are equally abundant, but it will be a useful summary statistic. Both p and u can be thought of as instantaneous-rate analogs of the population harvest rate and vulnerability scaled to per unit hunting effort. It is p and u that we will estimate. Harvest rates for both males and females (6) and vulnerability (5) may be obtained from these estimates.

The nonlinear least-squares procedure requires initial estimates of p and u. An initial estimate of the average harvest rate, eq. (4), is obtained from D. Fraser's (unpubl.) formula:

$$\text{Average harvest rate} = \sim 1/(\textit{number of harvests before the sex ratio reaches } 1{:}\,1) \quad (7)$$

This estimate of the average harvest rate, divided by average effort, gives a reason-able initial value for p when the average harvest rate is small. An initial value for u is that value that equates the ratio $(p + u)/(p - u)$ to the ratio of males to females in the harvest during the first year or years of differential vulnerability. Alternatively, any reasonable trial values can be used. With these initial values for *p* and *u*, more accurate values can be obtained by an iterative process.

To avoid the skewness in the distribution of error inherent in ratio estimates (Fieller 1954, Draper and Smith 1966), we will estimate p and u by minimizing the difference between the logarithms of the observed and expected sex ratios by a nonlinear least-squares method. Let

$$y_i = \log \text{ of observed sex ratio}$$
$$= \ln(H_{m,1}/H_{f,i}$$

Replacing the parameters p_m and p_f with p and u from eq. (6), assuming $m_1 = f_1$, and taking the logarithms of both sides, eq. (3) may now be written to give the expected values

$$\begin{aligned} E(y_i) &= -2u \sum_{j=1}^{i-1} e_j \\ &\quad + \ln\{1 - \exp[-(p+u)e_i]\} \\ &\quad - \ln\{1 - \exp[-(p-u)e_i]\} \end{aligned} \tag{8}$$

The weight of the logarithm of each observed ratio value should be proportional to the inverse of its variance. The weights may be calculated in the following manner. Let n be the total number of animals sampled in a given year when the cohort that is being studied is in its i^{th} season, and $q_1 = H_{m,i}/n$ and $q_2 = H_{f,i}/n$. The estimated variance of $H_{m,i}$ is then $nq_1(1 - q_1)$, that of $H_{f,i}$ is $nq_2(1 - q_2)$ and their estimated covariance is $-nq_1q_2$. It can be shown by the use of the delta method (Deming 1964) that the variance of the logarithm of $H_{f,i}$ is $(1 - q_2)/nq_2$, that of $H_{f,i}$, is $(1 - q_2)nq_2$, and their co-variance is -1/n. Hence, the estimated variance of y_i is

$$\begin{aligned} \mathrm{Var}(y_i) &= (q_1 + q_2)/nq_1q_2 \\ &= (H_{m,i} + H_{f,i})/H_{m,i}H_{f,i} \ , \end{aligned}$$

and the estimated weights, w_i are

$$w_i = H_{m,i}H_{f,i}/(H_{m,i} + H_{f,i}) \ . \tag{9}$$

The weighted nonlinear least-squares procedure may now be applied to arrive at the best estimates of p and u using any of the readily available nonlinear least-squares computer programs. If a package such as BMDP3R (Dixon and Brown 1977) rather than BMDPAR is used, the derivatives of the right-hand side of eq. (8) with respect to p and u are also required. Before we actually used the non-linear least-squares procedure we simplified eq. (8) (Appendix). This makes the estimation procedure amenable to hand calculation.

The input data to a standard nonlinear least-squares program, such as BMDPAR, consist now of a series of values

$$y_i \ , \sum_{j=1}^{i-1} e_j \ , e_i \ , \text{and} \ \ w_i$$

along with the function specification, eq. (8). Alternatively, the procedure outlined in the Appendix may be used.

If data are available for several cohorts, a combined estimate with a considerably smaller variance is readily obtained sim-ply by combining all the years for which data are available, i.e., by calculating for each age and year the values of

$$y_i\,,\sum_{j=1}^{i-1} e_j\ ,e_i\,,\text{and}\ w_i$$

and entering these values into the program as if all were from 1 set of data.

Alternatively, the estimates may be based on the proportion of males in the harvest, i.e., on

$$p_i = H_{m,i}/(H_{m,i} + H_{f,i}) \tag{10}$$

and on its expected value, using a maximum-likelihood method. In trial calculations, both the maximum-likelihood method and the least-squares method gave much the same results. Because the nonlinear least-squares method was much cheaper to run than the maximum-likelihood method, further details on the latter are omitted.

The nonlinear least-squares method is easily modified to estimate p and u from the age and sex composition of a single year's harvest. For each age-group the hunting effort must be known for that cohort's entire history. The only change, then, is that the cumulative effort term Σe_j in eq. (8) must be reinterpreted in an obvious manner (last column, Table 2). For the ith age-group it is twice the cumulative hunting effort that was applied to that cohort in all previous years, plus the current year's hunting effort.

Table 1. Moose-harvest data from Thunder Bay District, Ontario, for the cohort born in 1963, and estimation of harvest rate using the nonlinear least-squares method.

		Harvest		
Year	Hunting effort[a]	Age (years)[b]	Males	Females
1964	4.63	1.5	23	14
1965	5.32	2.5	31	12
1966	6.51	3.5	39	19
1967	7.36	4.5	43	34
1968	5.52	5.5	26	18
1969	7.12	6.5	21	20
1970	5.94	7.5	15	16
1971	5.98	8.5	12	14
1972	7.80	9.5	17	13

$\hat{p} = 0.0230$ $\quad \hat{\text{var}}(\hat{p}) = 2.07 \times 10^{-5}$

$\hat{u} = 0.0081$ $\quad \hat{\text{var}}(\hat{u}) = 0.735 \times 10^{-5}$

$\hat{\text{cov}}(\hat{p},\hat{u}) = 1.07 \times 10^{-5}$

Mean effort ($\bar{e}$) = 6.24 thousands of hunters.

Estimated average annual harvest rate of males = $(\hat{p} + \hat{u})\bar{e}$ = 0.193 (17.6% harvested annually).

Estimated average annual harvest rate of males = $(\hat{p} - \hat{u})\bar{e}$ = 0.093 (8.9% harvested annually).

[a] Thousands of hunters, estimated from a hunter survey.

[b] Ages estimated by the incisor-cementum method in 1971 and 1972, and by conversion from wear classes in other years.

RESULTS AND DISCUSSION

Typical cohort harvest data from the Thunder Bay district in Ontario were used for examples (Tables 1, 2). This method was applied to data in both Tables 1 and 2. The estimated harvest rates were 17.6 and 16.6% for males and 8.9 and 11.6% for females.

Table 2. Moose-harvest data from Thunder Bay District, Ontario, for the 1972 hunting season, and estimation of harvest rate using the nonlinear least-squares method.

Age[a] (years)	Males	Females	Year of entry[b]	Hunting effort in year of entry[c]	Cumulative effort[d]
1.5	131	107	1972	7.80	7.80
2.5	104	65	1971	5.98	19.76
3.5	63	40	1970	5.94	31.63
4.5	25	20	1969	7.12	45.88
5.5	20	14	1968	5.52	56.91
6.5	18	20	1967	7.36	71.63
7.5	15	12	1966	6.51	84.65
8.5	10	11	1965	5.32	95.29
9.5	17	13	1964	4.63	104.54
10.5	9	17	1963	4.73	113.99
11.5	6	5	1962	4.70	123.39
12.5	3	6	1961	3.76	130.91
13.5	4	3	1960	3.23	137.37
14.5	2	2	1959	2.40	142.16

$\hat{p} = 0.0195$ $\quad \widehat{\text{var}}(\hat{p}) = 3.90 \times 10^{-5}$

$\hat{u} = 0.0037$ $\quad \widehat{\text{var}}(\hat{u}) = 0.275 \times 10^{-5}$

$\widehat{\text{cov}}(\hat{p},\hat{u}) = 0.913 \times 10^{-5}$

Effort (*e*) in 1972 = 7.80 thousands of hunters.

Estimated harvest rate of males in 1972 = $(\hat{p} + \hat{u})e$ = 0.181 (16.6% harvested).

Estimated harvest rate of females in 1972 = $(\hat{p} - \hat{u})e$ = 0.123 (11.6% harvested).

[a] Estimated by the incisor-cementum method.

[b] Year of entry (at age 1.5 years) to the population harvested with bias toward males.

[c] Thousands of hunters, estimated from a hunter survey.

[d] Cumulative effort is the current year's effort plus twice the total effort in all previous years since year of entry at age 1.5 years.

To verify the method, a Monte Carlo study was conducted using simulated data. We started with a fixed number of males and females in a cohort and chose fixed values for p, u, and S_a. Hunting effort was kept constant. The harvest rates for males and females were then calculated from the assigned values of p and u. Using harvest rates and the annual survival as probabilities, random numbers were generated to determine whether a particular moose was taken by hunters, died when the season was closed, or survived to the next season. In this way, randomly fluctuating harvest data were simulated and then used as input for a program to estimate the parameters for 1 cohort harvested for 10 years (Table 3). Actual *p* and *u* values are presented with their estimates, variance and co-variance, by the nonlinear least-squares method. Actual values of *p* and *u* are compared with the averages of their nonlinear least-squares estimates for a range of values of *p* and *u* (Table 4). Each average is based on 100 simulated cohorts.

In addition to the estimates of variance returned by the least-squares program, we listed estimates of the true variance calculated from the 100 estimates of *p* and *u* around their known values (Table 4). The latter variances tend to be smaller than those returned by the least-squares method. Hence, the confidence limits of $\hat{p}$ and $\hat{u}$ that would normally be constructed from these variances are conservative, i.e., confidence levels tend to be higher than the stated level. The reliability of the estimates, judged on the basis of their variances, generally decreases as the difference in vulnerability (u) decreases. When $u = 0$, the method breaks down.

Table 3. Example of simulated data and resulting estimates for a cohort with initial population size of 500 males and 500 females. Nonhunting survival S set at exp (-0.1) for both sexes and hunting effort of 1,000 hunters each year, with p = 0.12 and u = 0.05.

Year (i)	$H_{m,i}$	$H_{f,i}$	$H_{m,i}$ / $H_{f,i}$	w_i	m_i + 1	f_i + 1
1	83	41	2.02	27.44	373	418
2	58	27	2.15	18.42	284	348
3	45	24	1.88	15.65	220	293
4	40	18	2.22	12.41	166	249
5	23	16	1.44	9.44	135	205
6	20	18	1.11	9.47	106	167
7	19	10	1.90	6.55	80	141
8	8	10	0.80	4.44	66	113
9	10	7	1.42	4.12	49	94
10	4	7	0.57	2.54	34	79

$\hat{p} = 0.116$ $\quad \widehat{\text{var}}(\hat{p}) = 6.75 \times 10^{-4}$

$\hat{u} = 0.046$ $\quad \widehat{\text{var}}(\hat{u}) = 2.03 \times 10^{-4}$

R^2 [a] $= 0.57$ $\quad \widehat{\text{cov}}(\hat{p},\hat{u}) = 3.49 \times 10^{-4}$

[a] R^2 equals the summed squares due to regression divided by total summed squares.

Table 4. Summarized results of Monte Carlo simulations, showing actual values of p and u, the estimated values of $\hat{p}$ and $\hat{u}$, their variances and covariance estimated by the regression program, and estimates of the true variances. Each line gives average values for 100 simulated cohorts, each beginning with 500 males and 500 females.

p	u	$\hat{p}$	$\hat{u}$	$\widehat{\text{Var}}(\hat{p})$[a] $\times 10^4$	$\widehat{\text{Var}}(\hat{u})$[a] $\times 10^4$	$\widehat{\text{Cov}}(\hat{p},\hat{u})$[a] $\times 10^4$	R^2	$\widehat{\text{Var}}(\hat{p})$[b] $\times 10^4$	$\widehat{\text{Var}}(\hat{u})$[b] $\times 10^4$
0.100	0.035	0.104	0.039	17.41	3.69	7.32	0.38	11.62	3.18
0.100	0.050	0.099	0.050	9.73	3.85	5.82	0.48	8.02	3.30
0.100	0.065	0.104	0.069	7.32	4.64	5.58	0.58	7.33	5.05
0.120	0.035	0.126	0.039	20.09	3.20	7.01	0.41	13.75	2.97
0.120	0.050	0.115	0.050	12.23	3.59	6.08	0.49	10.34	3.65
0.120	0.065	0.118	0.065	8.29	4.15	5.57	0.57	6.46	3.32
0.140	0.035	0.137	0.036	30.42	3.20	8.33	0.37	16.06	2.32
0.140	0.050	0.137	0.049	14.06	3.28	5.98	0.50	9.00	2.65
0.140	0.065	0.135	0.064	8.70	3.38	4.94	0.62	7.55	3.49
0.160	0.035	0.160	0.032	33.62	2.85	7.68	0.41	19.51	2.75
0.160	0.050	0.158	0.052	15.18	3.05	5.67	0.54	11.70	2.91
0.160	0.065	0.155	0.063	19.00	3.24	4.97	0.61	6.66	2.42
0.180	0.035	0.177	0.036	52.71	2.84	8.77	0.40	23.23	2.64
0.180	0.050	0.181	0.052	17.77	2.82	5.50	0.56	9.70	2.14
0.180	0.065	0.175	0.063	11.79	3.09	4.95	0.63	8.45	2.91
0.200	0.035	0.200	0.036	48.84	2.79	7.90	0.50	26.42	1.74
0.200	0.050	0.195	0.050	25.57	3.22	6.65	0.52	16.54	2.94
0.200	0.065	0.197	0.064	14.64	3.18	5.28	0.63	10.13	2.81

[a] Average of the estimates given by the nonlinear least-squares program.

[b] Calculated from the 100 estimates of $\hat{p}$ and $\hat{u}$ around their known value.

We have also examined the effect of bias in the estimates caused by deviation from a 1:1 sex ratio at the beginning of the first year of harvesting (Table 5). Over most of the range of values shown, the bias in $\hat{p}$ is

roughly similar in size to the bias in the initial sex ratio. When males are initially more abundant than females, p is underestimated; when males are less abundant, p is overestimated. As the deviation from the 1:1 sex ratio increases, the bias in $\hat{p}$ and its variance gets progressively larger, especially when u is small or when the females are more abundant than the males. The estimate of the vulnerability, u, does not seem to be greatly affected by initial abundance.

Table 5. The effect of departure from a 1:1 initial sex ratio on estimated $\hat{p}$ and $\hat{u}$, and their variance and covariance, in Monte Carlo simulations. Cohorts began with 500 females and 500*b* males, where *b* is the bias factor. Each line gives average values for 100 simulated cohorts with *b*, *p*, and *u* as listed.

b	*p*	*u*	$\hat{p}$	$\hat{u}$	$\widehat{\mathrm{Var}}(\hat{p})$[a] × 10^4	$\widehat{\mathrm{Var}}(\hat{u})$[a] × 10^4	$\widehat{\mathrm{Cov}}(\hat{p},\hat{u})$[a] × 10^4	R^2
1.2	0.10	0.035	0.088	0.041	11.53	3.47	6.01	0.41
1.2	0.10	0.050	0.091	0.053	8.29	3.97	5.56	0.50
1.2	0.10	0.065	0.093	0.065	6.86	4.49	5.45	0.56
1.2	0.15	0.035	0.111	0.036	18.34	2.70	6.38	0.41
1.2	0.15	0.050	0.121	0.052	9.73	2.92	4.90	0.56
1.2	0.15	0.065	0.132	0.067	7.00	3.19	4.42	0.65
1.2	0.20	0.035	0.133	0.036	23.13	2.61	6.78	0.42
1.2	0.20	0.050	0.147	0.049	13.92	2.82	5.51	0.53
1.2	0.20	0.065	0.157	0.063	8.82	2.65	4.31	0.66
1.1	0.10	0.035	0.087	0.034	15.27	3.39	6.82	0.34
1.1	0.10	0.050	0.094	0.051	10.54	4.24	6.41	0.46
1.1	0.10	0.065	0.105	0.073	6.90	4.68	5.54	0.61
1.1	0.15	0.035	0.119	0.034	22.69	2.94	7.28	0.36
1.1	0.15	0.050	0.130	0.049	12.70	3.11	5.67	0.51
1.1	0.15	0.065	0.133	0.061	7.22	2.80	4.16	0.64
1.1	0.20	0.035	0.152	0.034	36.64	2.76	8.36	0.37
1.1	0.20	0.050	0.171	0.052	14.92	2.63	5.19	0.58
1.1	0.20	0.065	0.172	0.063	11.39	3.04	4.99	0.65
0.9	0.10	0.035	0.115	0.036	23.77	3.54	8.04	0.34
0.9	0.10	0.050	0.110	0.052	12.06	4.22	6.66	0.47
0.9	0.10	0.065	0.106	0.065	8.58	4.96	6.31	0.54
0.9	0.15	0.035	0.198	0.039	46.79	3.05	7.68	0.41
0.9	0.15	0.050	0.174	0.049	22.74	3.32	6.62	0.49
0.9	0.15	0.065	0.167	0.066	11.53	3.54	5.36	0.62
0.9	0.20	0.035	0.288	0.035	294.80	3.01	5.91	0.38
0.9	0.20	0.050	0.244	0.050	43.57	3.08	5.84	0.53
0.9	0.20	0.065	0.225	0.062	20.05	3.05	5.04	0.62
0.8	0.10	0.035	0.136	0.035	37.70	4.12	10.03	0.30
0.8	0.10	0.050	0.120	0.052	16.00	4.37	7.47	0.47
0.8	0.10	0.065	0.117	0.069	10.04	5.75	7.27	0.52
0.8	0.15	0.035	0.308	0.034	559.90	3.07	–0.04	0.36
0.8	0.15	0.050	0.221	0.055	28.69	3.39	5.20	0.56
0.8	0.15	0.065	0.190	0.065	13.30	3.45	4.89	0.62
0.8	0.20	0.035	0.630	0.036	[b]	3.05	[b]	0.38
0.8	0.20	0.050	0.408	0.049	[b]	3.42	[b]	0.47
0.8	0.20	0.065	0.290	0.064	44.54	3.54	4.10	0.60

[a] Estimates given by the nonlinear least-squares program.

[b] The program failed to produce reasonable estimates of the variance and covariance.

Because this method uses data from a number of years or cohorts, certain changes over time in the population can cause spurious results. The initial sex ratio and the differential vulnerability of the sexes should not change systematically over the years in question. Also, differential vulnerability of the sexes should not change systematically with age for the range of ages used.

Unpublished moose-harvest data from Ontario indicate that the method is generally applicable. However, if the opening date of the hunting season is made progressively earlier or later over several years, male vulnerability may be altered systematically, producing incorrect results. In lightly hunted areas, the greater vulnerability of males begins at age 2.5 years instead of 1.5 years. In this case, the 1.5-year-olds should be omitted from the analysis. Changing patterns of hunter access may cause hunting pressure to shift from place to place over years with-in a given management area. Such movement invalidates virtually all use of age and sex data, and can be remedied only by more precise geographic delineation of populations.

The number of hunters was used as a measure of hunting effort because it was the only suitable measure determined for all years included in the examples (Tables 1, 2). More precise measures, such as hunter-days, would be preferable if they were available.

Like moose, white-tailed deer (*Odocoileus virginianus*) show a gradual change with age in the sex ratio of the harvest. However, some biologists attribute this to age-specific changes in the differential vulnerability of the sexes with age (R. Hepburn, pers. commun.) and to differential rates of nonhunting mortality, both of which would invalidate the type of analysis described here. Further testing of the assumptions is needed for moose, white-tailed deer, and other species. We strongly discourage indiscriminate use of the method, as is so often done with life tables and other estimates of mortality.

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APPENDIX

Initially we looked at both the nonlinear least-squares and maximum-likelihood methods. However, the computational load using the 1st method is less than using the 2nd. Because the estimates by the 2 methods are comparable, only the least-squares method is given here.

Expanding the exponential function as a power series retaining the first 3 terms, and then using the approximation In $x(1 + x)$ = In $x + x$, valid for small values of x, the last 2 terms of (8) may be approximated by a simple expression. By denoting the right-hand side of eq. (8) as $F(p, u, i)$ we get:

$$F(p,u,i) = -u(2\sum_{j=1}^{i-1} e_j + e_i) + \mathrm{In}[(p+u)/(p-u)]. \quad \text{(A1)}$$

The derivatives of F can now be written:

$$F'_p = \partial F(p,u,i) \,/\, \partial p = 1/(p+u) - 1/(p-u) \quad \text{(A2)}$$

$$F'_u = \partial F(p,u,i) \,/\, \partial u = 1/(p+u) - 1/(p-u) - (2\sum_{j=1}^{i-1} e_j + e_i)$$

Whether the derivatives of the original eq. (8) or of its approximation (A1) are used makes little difference in the final results. The approximation (A1), however, is somewhat easier to implement on a smaller computer. If eq. (A1) is used in a nonlinear least-squares program the input values are y_i, w_i, and, instead of

$$\sum_{j=1}^{i-1} e_j$$

and e_i required by eq. (8),

$$2\sum_{j=1}^{i-1} e_j + e_i$$

On a smaller computer the nonlinear least-squares program may not be available. The weighted linear-regression formulae may, however, be applied iteratively to arrive at the estimates of p and u. The usual formulae have to be adjusted to take account of the fact that the constant term, typically present in linear regression, is absent. The final formulae are

let

$$
\begin{aligned}
A &= \Sigma\, w_i (F'_p)^2, \\
B &= \Sigma\, w_i F'_p F'_u, \\
C &= \Sigma\, w_i (F'_u)^2, \\
D &= \Sigma\, w_i F'_p\, \delta y_i, \text{ and} \\
E &= \Sigma\, w_i F'_u\, \delta_i
\end{aligned}
\tag{A3}
$$

Where δy_i stands for the difference between the logarithm of the observed sex ratio and its expected value (A1), and where the derivatives F'_p and F'_u are evaluated at current values of $\hat{p}$ and $\hat{u}$. The summations range over the years for which data exist. The adjustments to $\hat{p}$ and $\hat{u}$, Δp and Δu, are now calculated from

$$
\begin{aligned}
\Delta p &= (DC - EB)/Det, \quad \text{and} \\
\Delta u &= (EA - DB)/Det
\end{aligned}
$$

where

$$Det = AC - B^2.$$

The corrections are made in $\hat{p}$ and $\hat{u}$, and the new values of $\hat{p}$ and $\hat{u}$ are substituted in the equations for y_i, F'_p, F'_u. Then $\hat{p}$ and $\hat{u}$ are reevaluated until the correction terms are small enough. The variance and covariance are estimated during the final iteration from

$$
\begin{aligned}
\hat{\text{var}}(\hat{p}) &= CR/[(N-2)Det], \\
\hat{\text{var}}(\hat{u}) &= AR/[(N-2)Det], \text{ and} \\
\hat{\text{cov}}(\hat{p},\hat{u}) &= -BR/[(N-2)Det]
\end{aligned}
\tag{A4}
$$

where

$$
\begin{aligned}
N &= \text{number of years considered, and} \\
R &= \text{residual sums of squares} \\
&= \Sigma\, w_i \delta y_i^2.
\end{aligned}
\tag{A5}
$$

The separate male and female mortality rates may also be calculated from (6), and their variances obtained from

$$\text{var}(\hat{p}_m) = \text{var}(\hat{p}) + \text{var}(\hat{u}) + 2\,\text{cov}(\hat{p},\hat{u})$$

$$\text{var}(\hat{p}_f) = \text{var}(\hat{p}) + \text{var}(\hat{u}) - 2\,\text{cov}(\hat{p},\hat{u}).$$